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Non-breeding fæder Ruffs *Philomachus pugnax* associate according to sex, not morphology

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Capsule Fæders (males that are female look-alikes) associate with males rather than females, at several different spatial scales.

Aims To test the prediction that the occurrence in space and time of fæders on ecological grounds should track that of females.

Methods The fraction of fæders was estimated in five morphometric data sets that were collected over four decades in four different countries in three different seasons (comprising 9133 Ruffs). The regression of fæder–female fractions was tested against the null model assuming that the number of fæders is 1.0% of females.

Results The fraction of fæders in catches averaged 1.03%, varying between 0.3% in autumn in the UK up to 0.85% in Sénégal in winter and 1.04% in The Netherlands in spring. On a stopover in The Netherlands the fraction decreased from 1.3% to 0.7% when the females started to arrive. At all four spatial and temporal scales the regression of fæder–female fractions deviated from the null model: we found high fractions of fæders in catches with low fractions of females, indicating that fæders rather associate with the larger-sized ‘normal’ males.

Conclusion We suggest that fæders spend the winter, and migrate with, the larger-sized lekking males, and we propose that any survival costs associated with the use of suboptimal habitats is compensated by higher reproductive success as sneakers on leks.

Sexual segregation outside the breeding season has been observed in many vertebrates (Ruckstuhl & Neuhaus 2005). In birds, the different sexes may enhance their survival by: (1) employing social dominance to exclude the other sex; (2) body size-specific specialization and distinct habitat use; (3) optimizing annual schedules, especially arrival time in the breeding areas (Catry *et al.* 2005, Ketterson & Nolan 1983, Myers 1981).

Ruffs *Philomachus pugnax* are strongly sexually dimorphic sandpipers in which the sexes segregate during most of the year. In winter most females occur in east Africa and southern Africa, whereas many males stay in Europe and west Africa (Gill *et al.* 1995, OAG Münster

1996, Pearson 1981). The two displaying male morphs, which are twice as large as the female, migrate ahead of the females (Jukema & Piersma 2000) to arrive at the breeding grounds early and establish their positions at leks (van Rhijn 1991). Males are not involved in brooding and parental care and leave the breeding areas before the females (Glutz von Blotzheim 1975, Hayman *et al.* 1986, Hogan-Warburg 1966, Lank *et al.* 1995, van Rhijn 1973). Females may take more easterly or inland migratory routes during northward migration (Jukema *et al.* 2001a, Karlionova *et al.* 2007, OAG Münster 1989a, 1989b, 1992, Wymenga 1999) and do not randomly mix with males at staging sites (Jukema *et al.* 2001a, Verkuil & de Goeij 2003). The sexual segregation in wintering and staging sites suggests that females not only have different migration schedules,

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but also distinct habitat preferences (Verkuil & de Goeij 2003).

Recently and rather surprisingly, the 'fæder' was discovered, a rare cryptic male morph with the plumage characteristics and body dimensions of females (Jukema & Piersma 2004, 2006). Fæders have a slightly different posture from females (Fig. 1), but otherwise cannot be distinguished from females. As they are so similar to females, we predicted that their use of habitat and their occurrence in space and time should track that of females. Here we test this hypothesis by looking at the associations between the relative occurrences of females and fæders at different spatial and temporal scales: (1) between catching sites throughout Europe and Africa; (2) between years within a catching site; and (3) during the season at a spring stopover site.

METHODS

Of the morphometrics routinely collected for Ruffs, only wing length shows complete discrete sexual dimorphism (Jukema *et al.* 1995, 2001a, Karlionova *et al.* 2007). Females have wing lengths of 150 to 170 mm, and displaying males 180 to 200 mm or more (Glutz von Blotzheim 1975, Jukema *et al.* 1995, 2001a, Jukema & Piersma 2006). Intermediate birds, with wing lengths between 170 and 180 mm and with female-like plumage characteristics, were assigned fæder status; molecular sexing of samples of such birds from the Dutch ($n = 22$) and Belarus ($n = 5$) migratory populations has confirmed them to be males (Jukema & Piersma 2004, Karlionova *et al.* 2007). Molecular sexing of males and females outside the size range of fæders confirmed that wing length is a sufficient diagnostic to assign sex and male type (Jukema & Piersma 2006).

We analysed five morphometric data sets that were collected over four decades in four different countries in three different seasons (Table 1). Catches of Ruffs were made with mist nets (in Sénégal, The Wash, UK, and The Netherlands), walk-in traps (in Pripyat,

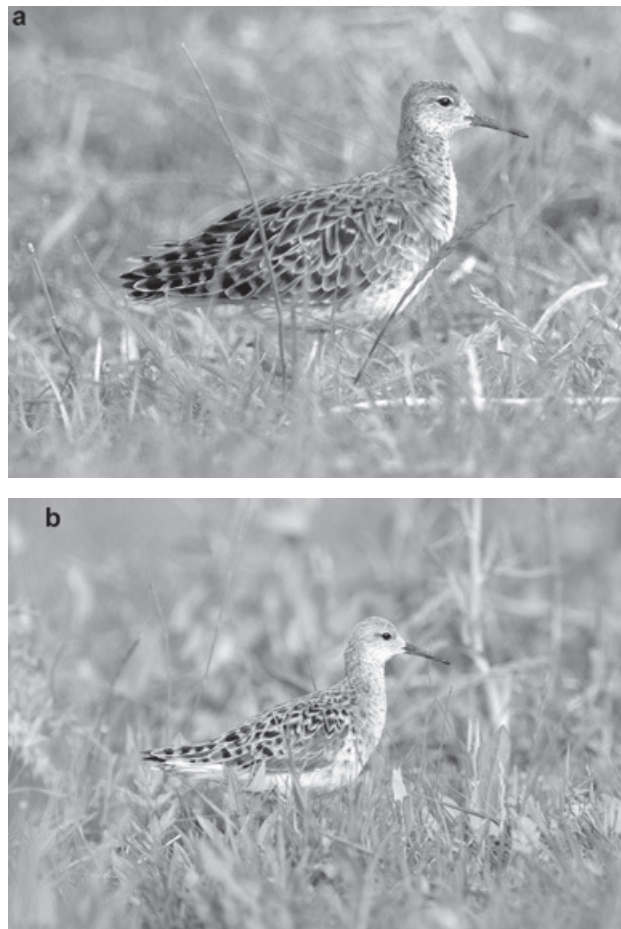


Figure 1. The fæder (a) can be distinguished from the female (b) by its slightly different posture and by the slightly bulkier body. Both birds were photographed in late April. Photo courtesy Richard Chandler.

Belarus) or wilsternets, a traditional netting method of Frisian wilsterneters (province of Fryslân, The Netherlands, Jukema *et al.* 2001b). In all data sets, wing length refers to measurements of the stretched but folded wing measured along a stopped ruler to the nearest millimetre by trained and experienced observers.

We test the following hypothesis: assuming that fæders associate with the females, the fraction of fæders

Table 1. Morphometric data sets used to obtain frequencies of fæders.

Country	Catching locality	Year	Season	<i>n</i>	References
Belarus	Pripyat valley	2001–05	Spring (April–May)	2225	Karlionova <i>et al.</i> (2007)
Sénégal	Sénégal delta	1985–88	Winter (November–March)	1406	OAG Münster (1996)
The Netherlands	Fryslân	2001–05	Spring (March–May)	3888	Jukema <i>et al.</i> (2001a)
The Netherlands	Fryslân	1974–2004	Spring–autumn (March–November)	1277	Koopman (1986)
United Kingdom	The Wash	1963–85	Autumn (July–October)	337	Gill <i>et al.</i> (1995)

in catches increases with an increasing fraction of females. To examine assumed fæder–female associations, we expressed the number of fæders in the data sets as a fraction of the number of males and regressed it against the fraction females/males and log-transformed for linearity. We tested this regression against the null model assuming that the number of fæders is 1.0% of females (Jukema & Piersma 2006). In this model, the (log-transformed) fraction of fæders increases linearly with an increase in the fraction of females with a slope of 1. Deviations would indicate that fæders actively avoid females and associate with males.

We tested our hypothesis under four conditions: during the winter, during the migration season, between years, and over the geographical range of the Ruff. The winter data were collected in Sénégal in 1985 and 1987/88 between November and March. We analysed the winter data by dividing the data into ten-day periods to provide sufficiently large sample sizes. The migratory data set consists of nine weeks of spring catches in southwest Fryslân in 2004 and 2005. Weekly catches ranged from 18 to 342. There was no correlation between weekly catch size and the percentage of fæders in catches ($F_{1,18} = 0.03$, $P = 0.87$). As the chances of encountering fæder phenotypes in small samples are very small, we omitted from the analyses all weeks with catch totals below 40. The annual data set included five years of catches in southwest Fryslân (2001–05). The geographical data set includes three localities in Europe and one in Africa (Table 1).

RESULTS

The overall occurrence of fæders in the 9133 Ruffs included in the present analysis was 1.03%. The frequency of fæders in the five data sets varied from 0.3% in autumn in the UK, to 0.85% in winter in Sénégal, up to 1.2% in the long-term Dutch data set (Fig. 2a). The frequencies in the migratory population in The Netherlands varied in 2001–05 between 0.7 and 1.3% (Fig. 2b), with an average of 1.04% (47 fæders in 3888 Ruffs).

In The Netherlands, the weekly percentage of fæders in the catches varied between 0.4% and 6.3% in 2004, and between 0.3% and 2.1% in 2005. In both years, the percentage significantly declined over the season (Fig. 2c). So as the relative number of females increased the percentage of fæders decreased.

At all four spatial and temporal scales, the regression between the fraction of fæders and females in the

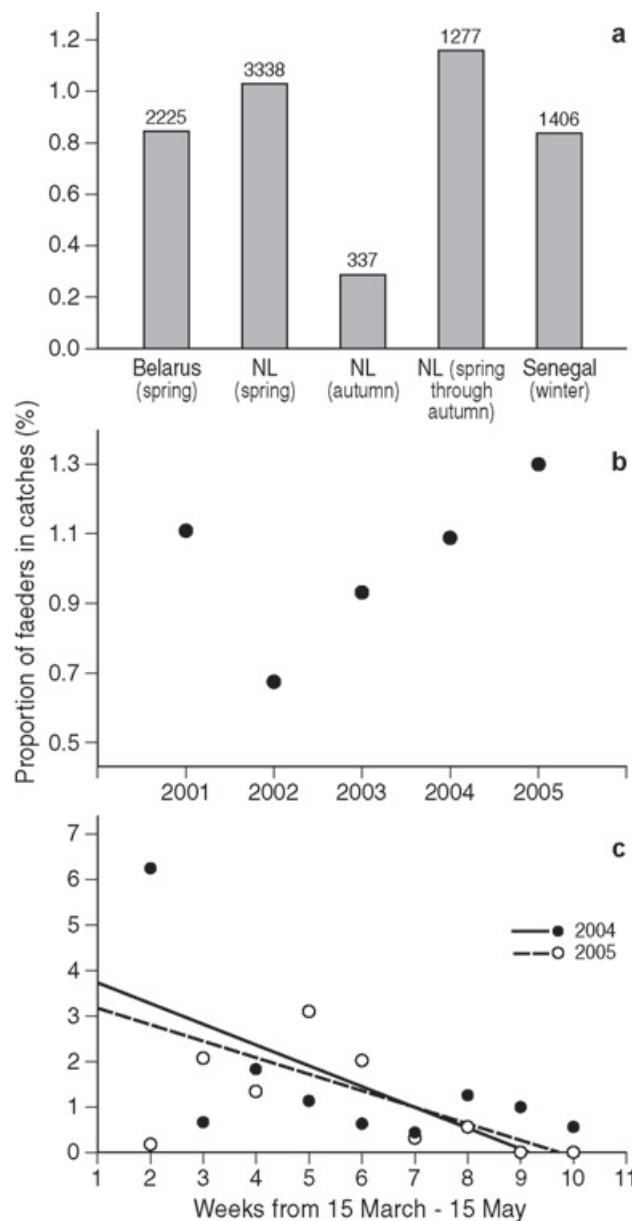


Figure 2. Frequency of fæders in catches. (a) At four staging and/or wintering sites in Europe and Africa. See Table 1 for further information. (b) Annual variation in 2001–05 in southwest Fryslân, The Netherlands, during spring migration. Total numbers of birds with known wing length were 180 (2001), 1031 (2002), 533 (2003), 1461 (2004) and 1301 (2005). (c) Seasonal variation during spring migration in southwest Fryslân, The Netherlands, in 2004 and 2005. The percentage significantly declined over the season (in a model with both year and week entered, only week was a significant factor $r^2 = 0.22$, $t_{11} = -2.7$, $P = 0.04$).

catches was tested against the null model assuming that the relative abundance of fæders follows that of females. On northward stopovers and among geographical catching localities, the slope of the regression of

the fraction of fæders against the fraction of females deviated significantly from the null model which has a slope of 1.

The data from the wintering area in west Africa and the annually collected Frisian data set showed the same trends, but the slopes were not significantly different from 1 (Fig. 3). For the combined data sets, the observed slope was 0.08, with a 95% confidence interval of -0.09 and 0.25 , and thus deviated significantly from the null model which has a slope of 1, indicating that fæders do not associate with females.

DISCUSSION

The observed frequencies of fæders fluctuated around an overall mean of 1.03%, which confirms that the fæder is a rare male morph (Jukema & Piersma 2004, 2006). We found no support for the idea that fæders, being morphologically similar to females, should associate with females. At all four spatial and temporal scales we found high fractions of fæders in catches with low fractions of females, indicating that fæders rather associate with the larger-sized 'normal' males. This observation was strongest in Ruffs in which the migration of males and females is staggered in time

(Jukema & Piersma 2000) and in Ruffs across geographical locations.

Although the proportions of females were not very variable on the final wintering destination in Sénégal, even here we observed that the fraction of fæders was higher than expected in periods with relatively low proportions of females. Fæder-lekking male associations thus extend as far as the west African wintering grounds. If the sexual segregation of Ruffs in winter indeed reflects habitat choice according to body size (including dominance effects), this would mean that fæders associating with males compromise winter survival.

The arrival time hypothesis states that individuals under greater pressure to arrive early at the breeding grounds winter closer to the breeding grounds. This would best explain why fæders associate with males during migration (Ketterson & Nolan 1983, Myers 1981), even if that involves the use of suboptimal stopover habitats. Arriving early on the breeding grounds, when the social relationships on the leks are established (Widemo & Owens 1995, Widemo 1997), may lead fæders to have a higher reproductive success than if they associated with females. We suggest that fæders, facing a trade-off between non-breeding survival and reproductive success, err in the direction of reduced survival.

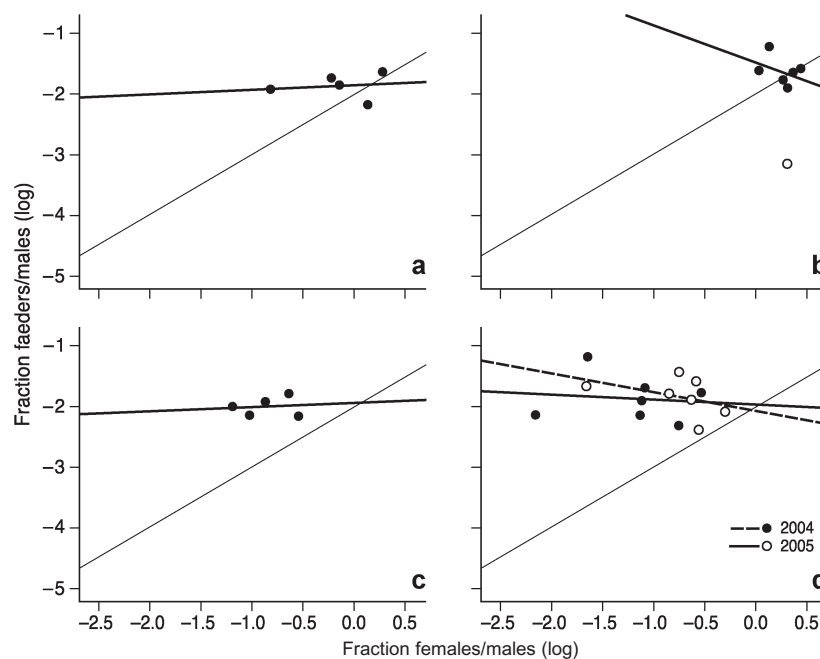


Figure 3. Correlation between fraction of fæders and females at four different spatial and temporal scales. The grey line indicates the expected relationship when the relative abundance of fæders is constant relative to females. For catching localities (a) and season (d), the slopes of the regressions were significantly different from 1 as the 95% CI did not include 1, being respectively 0.08 (95% CI, -0.8 to 0.96) and -0.13 (95% CI, -0.53 to 0.27). For year (c) and in Sénégal (b) the slope was not significantly different from 1 as the 95% CI included 1, being 0.07 (95% CI, -0.95 to 1.09) and -0.57 (95% CI, -2.38 to 1.25).

In the four data sets fæders were equally rare. This raises the question of whether we missed a proportion of fæders because we cannot distinguish them properly, or because they segregate from both females and males during winter and migration. We assigned fæders on the basis of wing length measurements. For the Dutch and the Belarus migrants, wing length has been proven to be diagnostic (Jukema & Piersma 2006). Of the Ruffs sexed molecularly, only those with wing lengths between 170 and 180 mm and with female plumage were molecular males. No fæders were found amongst smaller birds with female plumage, and neither did we observe any female plumage in the larger males that have been measured and ringed since the discovery of the fæder (>2000 individuals, pers. obs.). It also seems unlikely that we missed fæders because of biases related to observation or catching methods. In both The Netherlands and Belarus, 700–1200 Ruffs have been caught every spring for over five years, using two very different catching methods: wilsternets and walk-in traps. In both areas, catch size varies roughly between 1 and 50. We do catch female-only flocks, but we have never observed fæder flocks, which makes it unlikely that they migrate separately.

As discussed by Jukema & Piersma (2004, 2006), fæders are female mimics that may enact one of three alternative mating strategies: (1) ancestral caretaker; (2) co-operative satellite-like behaviour; or (3) sneaker male (Taborsky 1997, 2001, Sinervo & Zamudio 2001, Sinervo & Lively 1996). Ancestral males could be thought of as not mating on a lek and providing parental care, and it is difficult to see why it would be advantageous for them to associate with displaying males. Our finding that fæders associate with the larger lek-using males is consistent with either of the latter two evolutionary scenarios. In particular, if males maintain intra-sexual relationships throughout the year (Widemo 1997), there may be a positive balance between the success of obtaining fertilizations on the lek and reduced annual survival.

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anonymous referees. Since the 1980s Ulbe Rijpma has been one of the driving forces behind the transition that the traditional Frisian bird-catchers have made from hunting to catching for scientific purposes and he made years of biometrical data digitally available to us. He recently passed away and we dearly miss him. We dedicate this paper to his memory.

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